

SHOOT OR STAB? MORPHOLOGICAL EVIDENCE ON THE UNRESOLVED
OVIPOSITION TECHNIQUE IN *STYLOGASTER* MACQUART (DIPTERA:
CONOPIDAE), INCLUDING DISCUSSION OF BEHAVIORAL
OBSERVATIONS

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Abstract.—Behavioral observations on the oviposition behavior of *Stylogaster* are reviewed in combination with data on the egg morphology, egg placement, and the female postabdomen. The internal female reproductive tract of *S. stylosa* Townsend is described. While some behavioral observations seem to imply a shooting oviposition technique, the morphological evidence favors stabbing oviposition.

Key Words: Female postabdomen, oviscapt, female reproductive tract, spermathecae, eggs

In 1961 Rettenmeyer described the oviposition behavior of *Stylogaster* (Diptera: Conopidae) above swarms of raiding army ants (Hymenoptera: Formicidae, Ecitoninae) in Panama. "While hovering 30 to 70 cm above the ground, females of *Stylogaster* characteristically flipped their abdomens down, or their whole body shifted downward a few centimeters. This movement suggested that the flies were dropping or shooting eggs at the ants below" (p. 1004, emphasis mine). He further reported that on several occasions *Stylogaster* was seen to "dart after cockroaches."

Several other authors have also observed hovering *Stylogaster* above swarms of army ants in Central America (Fig. 1) or Africa: "occasionally one of the flies darting with great quickness toward the ground" (Bates 1863: 366); "now and again darting at them, without doubt for the purpose of ovipositing in their bodies" (Townsend 1897: 23); "suddenly pouncing down (apparently for the purpose of ovipositing)" upon fleeing cockroaches (Carpenter 1915, cited in

Stuckenberg 1963); or "pouncing like little warplanes amidst the ants" (Lindner 1955: 23, translated from German). Smith & Cunningham-van Someren (1985) observed that small cockroaches escaping from raiding army ants were attacked by *Stylogaster*. The closest observation was published by Lopes (1937: 260), who observed that some *Stylogaster* females approached an orthopteran and "with an extremely rapid movement inserted an egg in the abdomen between the tergites" (translated from Portuguese). Of the many documented observations none describes contact, grasping, or seizing of the victim.

The actual process of oviposition, i.e., how the egg is inserted into the host's body, remains obscure. Based on the investigation of collected material, Smith (1967: 52) speculated that "the eggs are probably laid by a stabbing movement of the abdomen, with the oviscapt thrust forward between the legs." He further surmised that "the hovering females frequently flick the tips of their abdomens rapidly, but it is doubtful if



Fig. 1. Hovering *Stylogaster* female, Los Alturas, Costa Rica.

oviposition accompanies this movement, since considerable force at close quarters must surely be needed for the egg to penetrate the host cuticle."

The present study follows up on this problem. Could it be, that (A) *Stylogaster* literally shoots eggs at its host, as suggested by the flipping movements of the abdomen (Rettenmeyer 1961) and the fact that no physical contact with the host has been reported? Or (B) are the eggs stabbed into the host's integument, as suggested by Smith (1967, 1979)? Or (C) are the eggs inserted more conventionally after the victim has been seized, which has so far escaped observation? The available information on the female postabdomen of *Stylogaster*, its dart-like eggs, and their random placement on the host's body is reviewed and supplemented by a description of the internal female reproductive tract of *S. stylosa* Townsend. The possibilities for shooting or stab-

bing oviposition in *Stylogaster* are weighed and approaches for further testing are suggested.

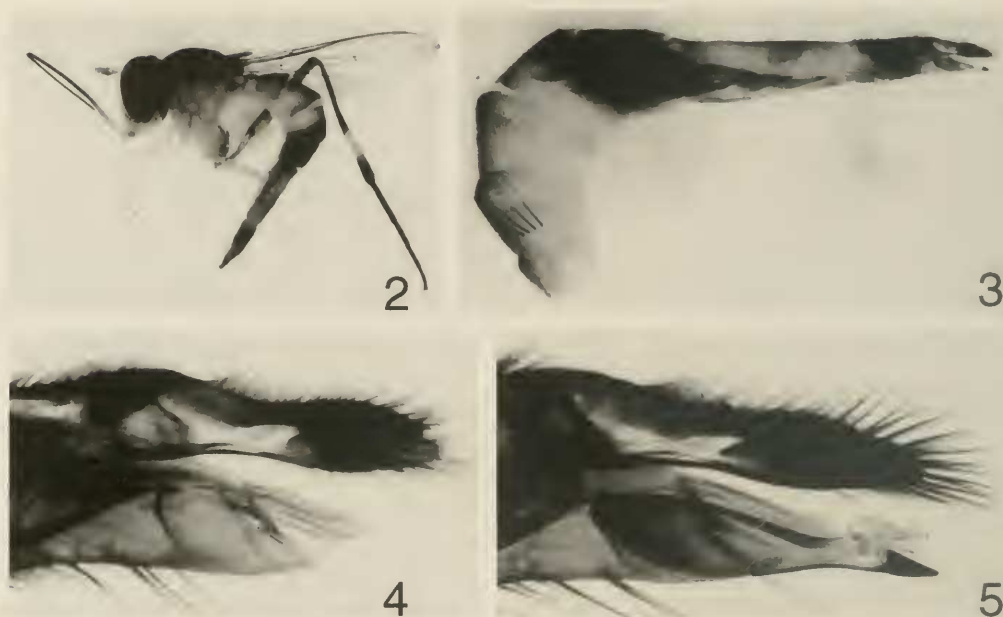
MATERIALS AND METHODS

The description of the internal female reproductive system of *Stylogaster* is chiefly based upon two specimens of *S. stylosa*, which were collected in Costa Rica and dissected immediately after killing. The female reproductive tract was removed, placed on a glass slide, and embedded in Polyvinyl-lactophenol with an admixture of Chlorazol E (Streng 1976). This medium slowly macerates the tissue while the dye is enriched in unsclerotized cuticle, staining it blue. The terminalia of *S. frauci* Smith were dissected while held in lactic acid. The preparations were investigated and documented with an Olympus BX50 compound microscope equipped with a drawing tube and Olympus SC35 camera, and with a Wild M 400 Photomakroskop.

RESULTS

Female Postabdomen

The female postabdomen of *Stylogaster* has been depicted for various species (Lopes 1937, 1938, 1971, Lopes and Monteiro 1959, Smith 1967, Smith and Peterson 1987). It is characterized by a tubular oviscapt (Smith 1966), which can be extremely long and narrow in some species (Figs. 2, 3). In the Brazilian *S. macrura* Lopes the oviscapt is twice as long as the remainder of the body excluding the antennae (Lopes 1938). The terminalia of *Stylogaster* lack any structures able to penetrate the host integument, as found in other Conopidae (Howell 1967, Smith & Peterson 1987) and other parasitic flies such as Pipunculidae (Hardy 1987) and Pyrgotidae (Steyskal 1987). Instead, the vulva is surrounded by various elongate structures ("egg guides" Smith 1979). The cerci are long and slender, the subanal plate is elongate. Sternum 8 ends in a pair of pointed lobes and bears a pair of long and slender lateral append-



Figs. 2-5. *Stylogaster frauci* female. 2. Total specimen in alcohol. 3. Abdomen cleared in lactic acid; eggs and spermathecae visible within the abdomen; one egg protruding from the vulva. 4. Terminalia. 5. Terminalia of with egg lodged in terminal chamber.

ages with inward curved endlobes (Figs. 4-9).

As reported above, *Stylogaster* females frequently "flip" the abdomen while in flight, rapidly flexing it under the body so that the oviscapt is directed anteroventrally. This movement is facilitated by the absence of sclerotized sternites in the first five abdominal segments (Stuckenberg 1963). The resulting flexed posture is often seen in pinned or preserved specimens (Fig. 2).

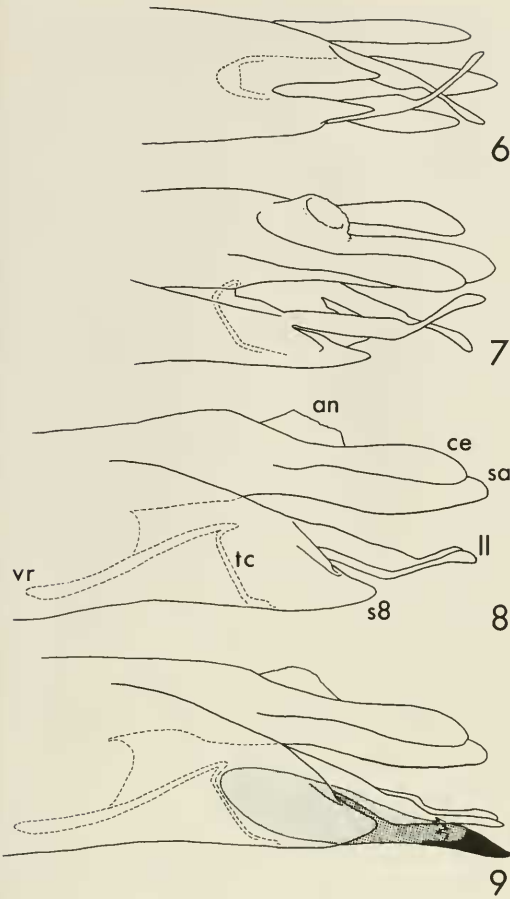
Egg

The eggs of *Stylogaster* show "remarkable adaptations for the penetration of, and retention in, the host cuticle" (Smith 1966: 264). They have been depicted for various species (Lopes 1937, 1938, 1971 Lopes and Monteiro 1959, Stuckenberg 1963, Smith 1967, 1979, Hinton 1981, Smith and Cunningham-van Someren 1985). In general *Stylogaster* eggs are elongate with a translucent brown chorion. The posterior end is black due to heavy sclerotization, sharply pointed, and bears up to four recurrent

spines (Figs. 5, 12). Moreover, a membranous bladder can be extruded from an area near the posterior end. This bladder is believed to be everted by osmosis after the egg is inserted into the host, serving to anchor the egg and erect the recurrent spines (Rettenmeyer 1961, Stuckenberg 1963). *Stylogaster* eggs are very different from those of other conopids, which have a thin whitish chorion, bear appendages at the anterior egg pole in the vicinity of the micropyle, and lack an extrusible bladder (de Meijere 1904, Smith and Peterson 1987).

Egg Placement on the Host Body

The accuracy of *Stylogaster* oviposition resembles that of a faulty shotgun. Stuckenberg (1963) and Smith (1967, 1969) found *Stylogaster* eggs to be positioned randomly on head, thorax, and abdomen of various muscids in South Africa, a few even in the wings. Stuckenberg (1963: 258) explained Rettenmeyer's (1961) findings of a nonrandom distribution of *Stylogaster* eggs on tachinids of the genus *Calodexia*



Figs. 6–9. Terminalia of *Stylogaster frauci*. 6, Ventral view. 7, View from upper left. 8, Lateral view (compare Fig. 4). 9, Lateral view with an egg lodged in the terminal chamber (compare Fig. 5). Abbreviations: an = anus; ce = cerci; ll = lateral lobes on sternum eight; sa = subanal plate; s8 = sternum eight; tc = terminal chamber; vr = sclerotized ventral rod.

Wulp from Panama as a result of “*Stylogaster* flies darting after cockroaches which were also being pursued by a number of *Calodexia*. If the tachinids were actively chasing the orthopterons, they would be more prone to receive a *Stylogaster* attack from behind owing to their forward motion which would necessitate some following by the *Stylogaster*, and also because the abdomen would be more susceptible owing to the attitude of the fly and more exposed as the wings would be in use.”

The accuracy of host choice seems like-

wise poor. *Stylogaster* eggs were found not only on members of the presumed hosts, entailing certain Orthoptera, Tachinidae, and silvicolous dung-breeding Muscidae (Lindner 1955, Rettenmeyer 1961, Stuckenberg 1963, Smith 1966, 1969, Smith and Cunningham-van Someren 1985), but on various other insects that might have been hit accidentally (Rettenmeyer 1961, Stuckenberg 1963, Smith 1966, Smith and Cunningham-Van Someren 1985). I even found a *Stylogaster* egg protruding from the median occipital sclerite of a *Stylogaster stylosa* female from Costa Rica.

Internal Female Reproductive Tract

The available information on the internal female reproductive tract of *Stylogaster* has been very limited. Lopes (1937) illustrated the spermathecal ducts of *S. stylata* (Fabricius) with a detail on the spermathecal duct pump. Moreover, Smith (1967) sketched the spermathecae of several African species. The present study of *S. stylosa* complements these data.

The internal female reproductive tract of *Stylogaster stylosa* (Fig. 10) comprises paired ovaries and lateral oviducts, a common oviduct, a tubular vagina, and a sclerotized terminal chamber. Into the dorsal wall of the vagina open two spermathecae, a third, blind duct between the spermathecae, a pair of accessory glands posterior to the spermathecae, and two additional, smaller evaginations, one anterior to the spermathecae and one posterior to the accessory glands. A roughly conical evagination emanates from the anteroventral portion of the vagina.

The ovaries usually contain a large number of mature and fully sclerotized eggs, but apparently no earlier egg stages. One of the *S. stylosa* specimens contained about 120 mature eggs. This is consistent with Smith's (1966, 1967) and Stuckenberg's (1963) findings of 60–128 mature eggs in African *Stylogaster*. Usually some eggs have already proceeded into the oviducts (Figs. 3, 12).

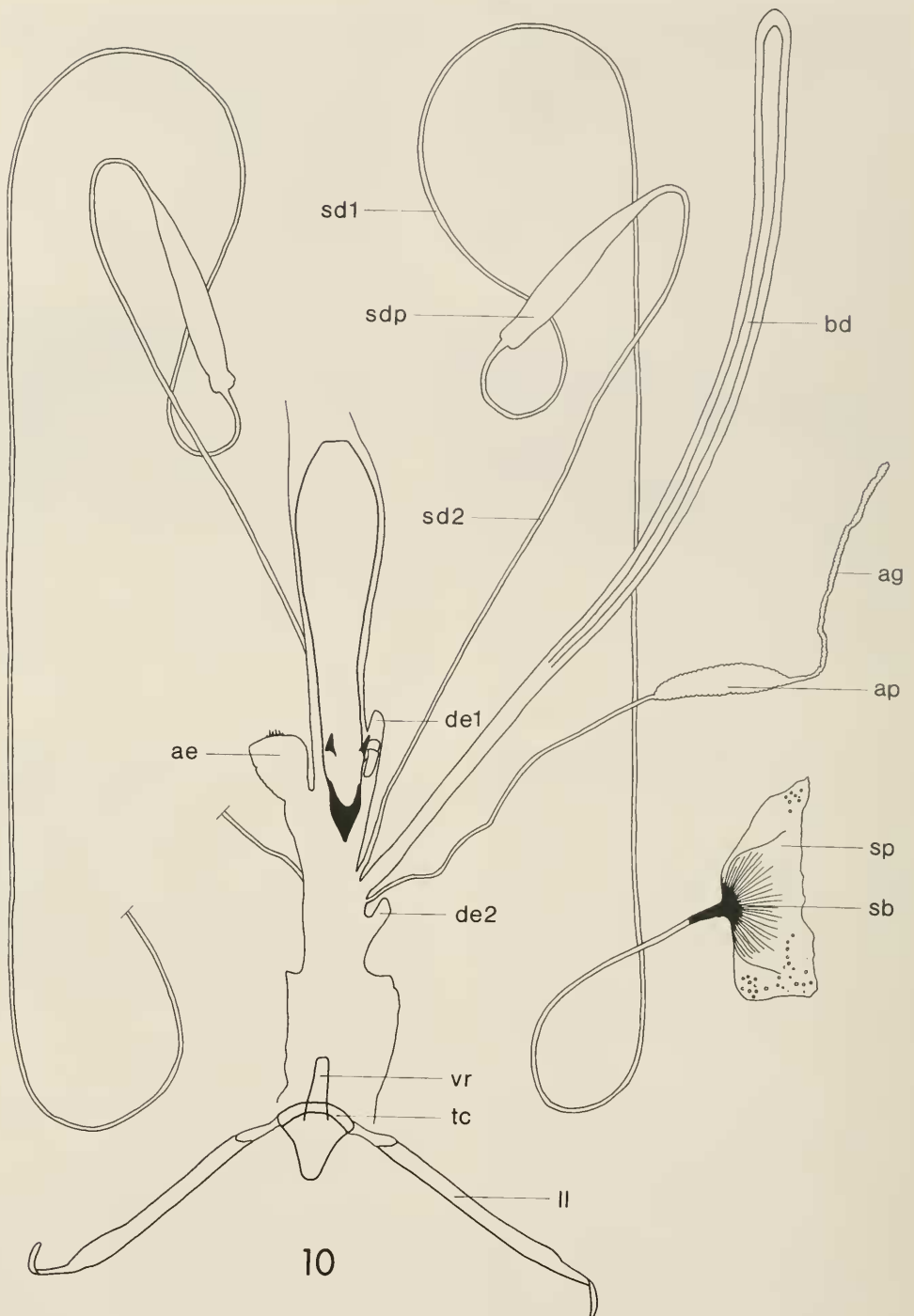
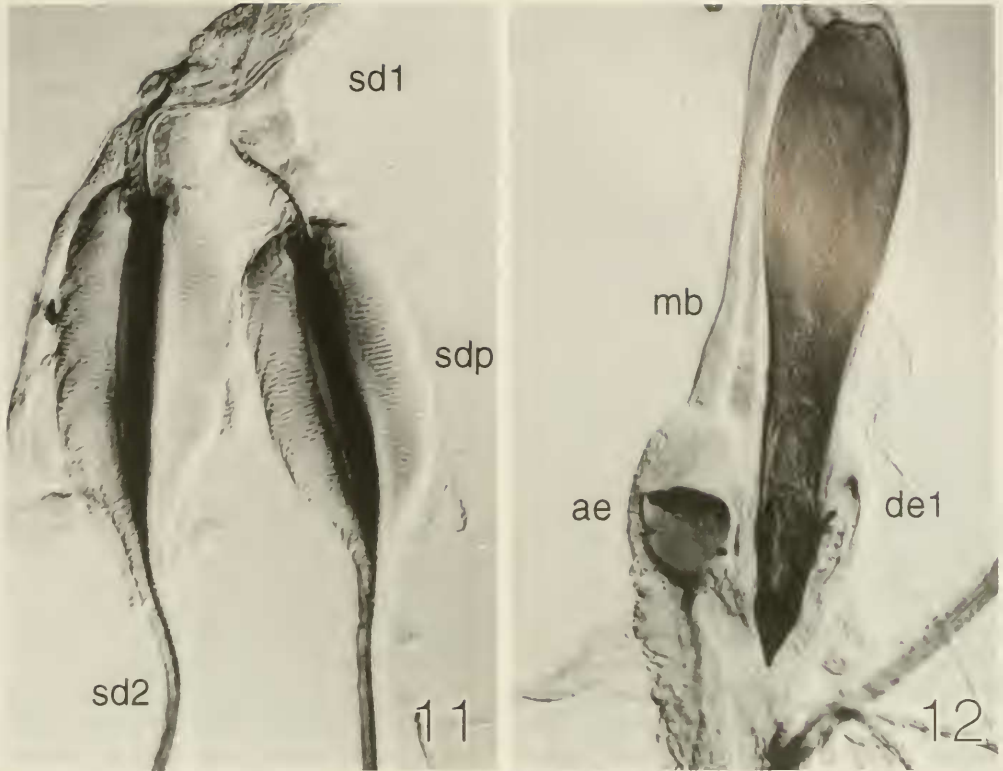


Fig. 10. Internal female reproductive tract of *Stylogaster stylosa*. Ovaries, one spermatheca, and one accessory gland omitted. Abbreviations: ae = anteroventral evagination; ag = accessory glands; ap = accessory gland pump; bd = blind duct; de 1, 2 = dorsal evaginations; ll = lateral lobes; tc = roof of the terminal chamber; sb = sclerotized base of the spermatheca; sd 1, 2 = apical and basal part of the spermathecal duct; sdp = spermathecal duct pump; sp = spermatheca; va = vagina; vr = sclerotized ventral rod.



Figs. 11–12. Internal female reproductive organs of *Stylogaster stylosa*. 11, Pump structure in the spermathecal ducts. 12, Common oviduct containing an egg and apical portion of the vagina. Abbreviations: ae = anteroventral evagination; de 1 = dorsal evagination; mb = muscle band extending anteriorly from the anteroventral evagination; sd 1 = apical part of spermathecal ducts; sd 2 = basal part of spermathecal ducts.

The two spermathecae are large, round, and almost entirely membranous. However, the spermathecal duct insertion at their base is surrounded by a small sclerotized area from which black spoke-like ridges radiate into the membranous part (Fig. 10). The spermathecal ducts are very long and thin, and show considerable differentiation along their length. The basal one-fourth consists of thick, colorless cuticle surrounded by a sheath of longitudinal muscles. The apical three-fourths consists of thinner, translucent brownish cuticle lacking a muscle sheath. Between the two portions there is an elaborate pump structure, consisting of a thick cuticular cylinder surrounded by a bulky layer of spiral muscles (Fig. 11). A third, blind duct is inserted between the two spermathecal ducts. It is only one-fourth of their

length, and its walls consist of thick, multi-layered rubber-like cuticle. The homology of this duct is unclear. The accessory glands have a tubular gland reservoir and membranous, narrow ducts, with a widened muscular pump region in their apical part.

The anteroventral evagination (Fig. 12) is thick-walled and surrounded by thick muscles like the rest of the vagina. Moreover, from its anterior wall a conspicuous muscle band extends anteriorly along the ventral side of the common oviduct. The homology of this anteroventral evagination is uncertain, although its position is reminiscent of the ventral receptacle of other acalyptrate Schizophora.

The membranous, tubular part of the vagina opens through a valve into a wider posterior portion, whose ventral wall is re-

inforced by a sclerotized rod. This rod connects posteriorly to the dorsal rim of a sclerotized oval terminal chamber that is invaginated from the posterior edge of sternum 8 (Figs. 4, 8, 9). In one of the specimens I found an egg fitted into this chamber, its pointed tip protruding from the vulva (Figs. 5, 9). I encountered the same condition in some dissections of *S. currani* Aldrich, *S. biannulata* Say, and *S. frauci*. Smith (1967) similarly figured a *S. leonum* Westwood specimen with the black, pointed tip of an egg protruding from the vulva. In *S. frauci* I could establish that the terminal chamber and surrounding sclerites have the same shape and position, whether containing an egg or not (Figs. 4, 5). There is no apparent evidence of elastic structures that might be able to store and rapidly release energy for the launching of an egg.

Dissections of other *Stylogaster* species show that the spermathecae, accessory glands, and additional dorsal evaginations vary considerably within the genus. These organs are not regarded in the following discussion and will be described in detail elsewhere. The constitution of the ovaries, the vagina, and the anteroventral evagination was found to be quite similar across the species, including African and Australian ones.

DISCUSSION

Three hypotheses regarding the ovipositional technique of *Stylogaster* were suggested in the Introduction: (A) shooting the eggs at the host from above with a flipping movement of the abdomen; (B) stabbing them into the host after a darting approach; and (C) the more conventional method of inserting an egg after seizing the victim. The Results section reviewed the available circumstantial evidence on the morphology of the female postabdomen, the eggs, and their placement in the host, and introduced new evidence regarding the morphology of the internal female reproductive tract. From this evidence the following inferences can be derived.

1. *Stylogaster* does not seize its host for oviposition. Otherwise the egg placement would be expected to be more precise, as is the case in other parasitic flies that seize their hosts, such as *Zodion obliquefasciatum* Macquart (Conopidae, Howell 1967). Oviposition on the head and wings would presumably be avoided in favor of locations, such as the abdomen, where the cuticle is thinner and the larva is likely to gain access to the body tissue. Moreover, grasping or seizing of the host has never been observed in *Stylogaster*. Therefore, the evidence does not support hypothesis C.

2. The penetration of the host cuticle must be achieved entirely by the tip of the egg itself. The terminalia of *Stylogaster* females lack any specialized piercing structures. Instead, the eggs show conspicuous adaptations for piercing, such as a strongly sclerotized and sharply pointed tip.

3. For stabbing oviposition, a fertilized egg would need to be pre-arranged and secured in such a manner, that its pointed tip protrudes from the female postabdomen. This is indeed the case. In several *Stylogaster* specimens, an egg was found in the appropriate position, with the anterior egg pole firmly lodged in the correspondingly shaped terminal chamber, and the posterior, pointed tip protruding from the vulva. It is hard to envision how this position can be achieved without the egg entirely slipping out of the vulva. Apparently the inward curved endlobes of the lateral appendages of sternum 8 take part in securing the egg.

4. On its way from the oviduct to the terminal chamber, the egg has to be fertilized. The anteroventral evagination of *Stylogaster* is similarly positioned and perhaps homologous to the ventral receptacle of other acalyptate Schizophora (Sturtevant 1925, 1926, Kotrba 1993) and the fertilization chamber of the Calyptrates (Leopold et al. 1978). It is conceivable that it likewise receives the anterior egg pole sometime during oviposition, possibly functioning as the fertilization site. The conspicuous muscle band that extends anteriorly from the

anteroventral evagination obviously pulls this organ into an anterior position while the vagina is extended. If the anteroventral evagination receives the egg in this position and the muscle band is relaxed subsequently, the egg will be propelled posteriorly by the elastic shortening of the extended vagina. Such a mechanism could considerably speed up the processes of fertilization and transportation of the egg.

5. If the egg is already positioned in the terminal chamber while the female is hovering with the ovipositor extended posteriorly (Fig. 1), then the frequently observed flicking movement of the postabdomen could be correlated with accelerating and/or launching the egg. The shooting hypothesis (A) matches the suppositions of some eye-witnesses and would account best for the random egg placement. The flicking of the abdomen is, however, unlikely to provide the necessary kinetic energy for the penetration of the host cuticle. So far, there are no clues to the presence of any other mechanism to accelerate the eggs.

6. In the case of stabbing oviposition (hypothesis B) the required energy could be derived from the stabbing impact, which might indeed be high due to the velocity of the approaching flight, described as "darting" or "pouncing" by eye-witnesses. Upon impact, the protruding posterior egg pole is thrust into the host cuticle while the anterior egg pole is prevented from giving way anteriorly by the sclerotized roof of the terminal chamber. After penetrating the host cuticle, the egg is locked by its recurrent barbs and pulled free of the oviscapt as the *Stylogaster* female flies away.

While this manuscript was being reviewed, Elke Buschbeck (personal communication) told me of an observation from Costa Rica that corroborates the latter scenario. She observed *Stylogaster* females hovering about 30 cm above the ground at the front of an army ant raid. One *Stylogaster* female darted down upon a cockroach, which was quickly running from one leaf to another for shelter. After an impact

of a fraction of a second the female flew away, and a light-colored object, presumably an egg, was visible sticking in the thorax of the cockroach.

CONCLUSIONS

Lacking detailed observations, the question of whether *Stylogaster* oviposits by shooting (hypothesis A) or stabbing (hypothesis B) can only be addressed through evaluation of circumstantial evidence. The present study favors the stabbing hypothesis suggested by Smith (1967, 1979). Stabbing is technically easier to conceive than shooting, and agrees well with the morphological evidence and some of the behavioral observations. However, even considering the high speed of a stabbing encounter, hypothesis B does not account as well for the poor egg placement on the host.

For a definitive answer, more detailed observations of oviposition in *Stylogaster* will be essential. This requires field work in South America or Africa, where *Stylogaster* can be seen ovipositing at the front of raiding army ant swarms. Alternatively, living *Stylogaster* females could be collected and provided with appropriate hosts, such as cockroach larvae or silvicolous dung-breeding Muscids, in a free-flying arena. In future investigations of the female postabdomen special attention should be given to structures that are apt to store and instantly release energy, such as parts of resilin or a notch and hook release mechanism.

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LITERATURE CITED

- Bates, H. W. 1863. The Naturalist on the River Amazon. First edition, Volume 2. Murray, London. vi + 423 pp.
- Carpenter, G. D. H. 1915. Dr. G. D. H. Carpenter's observations on *Dorylus nigricans* Illig., in Damba and Bugalla Islands. Proceedings of the Royal Entomological Society of London 1914: cvii-cxi.
- de Meijere, J. C. H. 1904. Beiträge zur Kenntnis der Biologie und der systematischen Verwandtschaft der Conopiden. Tijdschrift voor Entomologie 46: 144-225 + plates.
- Hardy, D. E. 1987. Pipunculidae, pp. 745-748. In McALPine, J. F., ed., Manual of Nearctic Diptera. Volume 2. Agriculture Canada, Research Branch (Monograph; No. 28), Ottawa.
- Hinton, H. E. 1981. Biology of insect eggs. 3 Volumes. Pergamon Press, Oxford. 1125 pp.
- Howell, J. F. 1967. Biology of *Zodion obliquefasciatum* (Macq.) (Diptera: Conopidae). Bulletin of the Washington Agricultural Experiment Station 51: 33 pp.
- Kotrba, M. 1993. Das Reproduktionssystem von *Cyrtodopsis whitei* Curran (Diopsidae, Diptera) unter besonderer Berücksichtigung der inneren weiblichen Geschlechtsorgane. Bonner zoologische Monographien 33: 115 pp.
- Leopold, R. A., S. Meola, and M. E. Degrugillier. 1978. The egg fertilization site within the house fly, *Musca domestica* L. (Diptera: Muscidae). International Journal of Insect Morphology and Embryology 7: 111-120.
- Lindner, E. 1955. Ostafrikanische Omphralidae. The-revidae und Conopidae (Dipt.). Jahresheft. Verein für Vaterländische Naturkunde in Württemberg 110: 19-23.
- Lopes, H. de Souza. 1937. Contribuição ao conhecimento do genero « Stylogaster » Macquart, 1835. Archivos. Instituto Biologica 3 (2): 257-293.
- . 1938. Sôbre uma nova espécie do genero *Stylogaster* Macquart, do Brasil. Memorias do Instituto Oswaldo Cruz 33 (3): 403-405 + 1 plate.
- . 1971. Notes on some old Species of *Stylogaster*, especially on paratypes of Aldrich's species (Diptera, Conopidae). Anais. Academia Brasileira de Ciências 43 (3/4): 691-710.
- , and L. Monteiro. 1959. Sôbre algumas espécies brasileiras de *Stylogaster* Macq., com a descrição de quatro espécies novas. Studia Entomologica 2 (1-4): 1-24.
- Rettenmeyer, C. W. 1961. Observations on the biology and taxonomy of flies found over swarm raids of army ants (Diptera: Tachinidae, Conopidae). The University of Kansas Science Bulletin 42 (8): 993-1066.
- Smith, K. G. V. 1966. The larva of *Thecophoa occi-densis*, with comments upon the biology of Conopidae (Diptera). Journal of Zoology, London 149: 263-276.
- . 1967. The biology and taxonomy of the genus *Stylogaster* Macquart, 1835 (Diptera: Conopidae, Stylogasterinae) in the ethiopian and malagasy regions. Transactions of the Royal Entomological Society of London 119 (2): 47-69.
- . 1969. Further data on the oviposition by the genus *Stylogaster* Macquart (Diptera: Conopidae, Stylogasterinae) upon adult calyptrate Diptera associated with ants and animal dung. Proceedings of the Royal Entomological Society of London (A) 44 (1-3): 35-37.
- . 1979. The genus *Stylogaster* (Diptera: Conopidae: Stylogasterinae) in the australian region. Australian Journal of Zoology 27: 303-310.
- , and G. R. Cunningham-van Someren. 1985. The larva of *Stylogaster varifrons* Malloch (Dipt., Stylogasteridae). Entomologist's Monthly Magazine 121: 81-85.
- , and B. V. Peterson. 1987. Conopidae, pp. 749-756. In McALPine, J. F., ed., Manual of Nearctic Diptera. Volume 2. Agriculture Canada, Research Branch (Monograph; No. 28), Ottawa.
- Steyskal, G. C. 1987. Pyrgotidae, pp. 813-816. In McALPine, J. F., ed., Manual of Nearctic Diptera. Volume 2. Agriculture Canada, Research Branch (Monograph; No. 28), Ottawa.
- Streng, R. 1976. Die Haarbalgmilbe des Menschen: *Demodex folliculorum*. Mikrokosmos 7: 202-205.
- Stuckenberg, B. R. 1963. A study on the biology of the genus *Stylogaster*, with the description of a new species from Madagascar (Diptera, Conopidae). Revue de Zoologie et de Botanique Africaines 28: 251-275.
- Sturtevant, A. H. 1925. The seminal receptacles and accessory glands of the Diptera, with special reference to the Acalypterae. Journal of the New York Entomological Society 33: 195-215.
- . 1926. The seminal receptacles and accessory glands of the Diptera, with special reference to the Acalypterae. Journal of the New York Entomological Society 34: 1-21 + plates 1-3.
- Townsend, C. H. T. 1897. Contributions from the New Mexico Biological Station—No. 2. On a collection of Diptera from the lowlands of the Rio Nautla, in the State of Vera Cruz. 1. Annals and Magazine of Natural History (6) 19: 16-34.